

Sexual Dimorphism of Head Size in *Phrynocephalus przewalskii*: Testing the Food Niche Divergence Hypothesis

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Abstract Sexual size dimorphism (SSD) is a general phenomenon in lizards, and can evolve through sexual selection or natural selection. But natural selection, which was thought to operate mainly through reducing the competition between the two sexes (niche divergence hypothesis), gave rise to a lot of controversy. We tested the niche divergence hypothesis in the toad-headed lizard *Phrynocephalus przewalskii* by comparing diet composition and prey sizes between males and females. The species was found to be sexual dimorphic, with males having relatively larger snout-vent length, head width, head length, and tail length, while females have relatively larger abdomen length. Based on analysis of 93 studied stomachs, a total of 1359 prey items were identified. The most common prey items were formicid, lygaeid and tenebrionid. The two sexes did not differ in the relative proportions of prey size categories they consumed and the dietary overlap based on prey species was high ($O = 0.989$). In addition, the meal size, the volume or any maximal dimension of the largest prey item in the stomach was not explained by the sexes. According to our results, food niche divergence might not play an important role in the SSD evolution of *P. przewalskii*.

Keywords *Phrynocephalus przewalskii*, sexual size dimorphism, niche divergence, food composition, prey size

1. Introduction

Sexual size dimorphism (SSD) is a general phenomenon in animals and is thought to evolve through several selection pressures (Cox *et al.*, 2003, 2007; Hedrick and Temeles, 1989). Sexual head size dimorphism is common in lizards, and males usually have larger heads than females (Herrel *et al.*, 1999, 2010; Lappin and Husak, 2005; Vanhooydonck *et al.*, 2010; Zhang *et al.*, 2005). This pattern can be explained by non-exclusive selection pressures, such as the difference of mating success between large and small males (Darwin, 1871), and niche divergence between the sexes to reduce intersexual competition (Schoener, 1967; Schoener, 1968; Shine, 1989). The former was the prevalent interpretation and supported elsewhere. The latter, however, was more controversial with inconsistent conclusions in previous studies (Herrel *et al.*, 2008; Verwaijen *et al.*, 2002; Gifford and Powell, 2007; Johnson *et al.*, 2005).

Researchers mainly focused on the role of SSD in

reducing food competition between the sexes when considering niche divergence (Schoener, 1967). In reptiles, head size determines the gap size and thus the size of the potential prey. This is evident in species which swallow the whole prey such as snakes (Vincent *et al.*, 2004). Moreover, sexual divergence in relative head size results in different bite force (Herrel *et al.*, 1999; Herrel *et al.*, 2010; Vanhooydonck *et al.*, 2010), which might affect the size of the potential prey. The niche divergence hypothesis has been challenged due to the ambiguous relationship between SSD and niche divergence, and some species exhibit niche divergence without SSD or exhibit SSD without niche divergence (Gifford and Powell, 2007; Johnson *et al.*, 2005).

The toad-headed lizards, *Phrynocephalus przewalskii*, occur along a wide geographical range in northern China and the adjacent Mongolia, and have been subjected to extensive systematic and ecological studies (Liu *et al.*, 1996; Urquhart *et al.*, 2009; Wang and Wang, 1993; Wang and Fu, 2004; Wang *et al.*, 2011; Xu and Yang, 1995; Zhao *et al.*, 2011). Previous studies indicated that juveniles of this species may reach sexual maturity within a year from birth and reach a snout-vent length (SVL) of 43 mm (Xu and Yang 1993, Liu *et al.*, 1996). Wang and Wang (1993) indicated that this species exhibited a male-

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biased sexual dimorphism in body size and proportionally hind leg length and inferred that this dimorphism was a result of sexual selection. However, the possible role of natural selection on head size dimorphism in this species has not been explored.

In this study, we examined the food composition, prey size and SSD in *P. przewalskii* and tested whether the observed size dimorphism can be explained by niche divergence. Examination of food niche divergence hypothesis is crucial for our understanding of the causal mechanism behind the maintenance of the sexual dimorphism, and also for future studies on morphology and ecology of the species.

2. Materials and Methods

Specimens of *P. przewalskii* were collected by hand from the Minqin Desert Experimental Research Station (38°38' N, 103°05' E) around Tengger desert in 2008 and 2009. The climate is arid (annual mean precipitation is 115 mm) and the predominant habitats are mobile dunes, semi-fixed dunes and fixed dunes (Zhao *et al.*, 2008). All captured individuals were marked by toe-clip. Most captured animals were used only for morphological data analyses and these individuals were released to the site where they were originally captured after being measured. Measurements included snout-vent length (SVL), head length (HL), head with (HW), and tail length (TL) and were taken by calipers. Adults were defined as those individuals having a SVL greater than 43 mm (Liu *et al.*, 1996). Measurements of abdomen length (AL, from the posterior base of the fore-limb to the anterior base of the hind-limb) were taken for 127 lizards which were captured in 2009.

Ninety-three individuals were euthanized using sodium pentobarbital in less than 1 h after capture and fixed in 5% formalin until stomachs were removed. Paired elements of prey (antenna, chelicera, telson, elytron) were separated and the largest number of elements from the left or right side was considered the number of individuals recovered from the sample. Prey items were identified to family by comparing the elements to the specimens preserved in the Museum of Lanzhou University. All prey items were individually measured (length and width), and the volume was calculated with the formula for the volume of an ellipsoid. According to the volume, we subdivided prey items into eight size classes (< 5 mm³, 5–10 mm³, 10–20 mm³, 20–30 mm³, 30–60 mm³, 60–100 mm³, 100–200 mm³, > 200 mm³).

We used the food niche breadth (FNB) method to

estimate dietary diversity, where $FNB = 1/\sum p_i^2$, and p_i is the proportion of prey category i in the samples from each sex (Levins, 1968). To compare dietary overlap, we used the formula:

$$O = \sum p_{ij} p_{ik} / (\sum p_{ij}^2 \sum p_{ik}^2)^{1/2},$$

where p_{ij} is the proportion of prey type i in one dietary sample and p_{ik} is the proportion of the same prey type in the other dietary sample (Pianka, 1973). All estimates of dietary diversity and overlap were based on prey numbers. Chi-square tests were used to test differences in prey composition and size between the sexes. Preys that belong to the same order were combined into analyses when the number of preys was less than 5.

To test the dietary divergence hypothesis, we followed the method described by Johnson *et al.* (2005). First, the relationship between meal size (the average volume of all prey items in the stomach) and body size was examined separately for males and females. For significant regressions, ANCOVA was performed to compare meal size between two sexes, otherwise ANOVA was used. We also performed a separate analysis to test if the sexes differed in any maximal dimension of the largest prey item in the stomach.

All data were tested for normality (Kolmogorov-Smirnov tests) and homogeneity of variances (Bartlett tests), and ln transformed when necessary to achieve the conditions for using parametric tests. Statistical test were performed using SPSS 19.0 for Windows. Mean values were expressed as mean \pm SE and $P < 0.05$ was considered as statistically significant.

3. Results

3.1 Sexual size dimorphism A total of 242 adult lizards were measured in this study and the largest male and female were 62.6 mm and 62.2 mm, respectively. Males are significantly larger than females in SVL (ANOVA, $F_{1,240} = 13.69$, $P < 0.001$). Male biased SSD was also found in HL, HW, and TL (ANCOVA, $P < 0.001$ in all cases) (Table 1). The rates at which HL, HW or TL

Table 1 Descriptive statistics of morphological traits for females (n = 130) and males (n = 112) of *Phrynocephalus przewalskii*.

Traits	Males	Females	ANOVA/ANCOVA
SVL (mm)	51.9 \pm 0.4	49.9 \pm 0.4	$F_{1,240} = 13.69$, $P < 0.001$
HL (mm)	13.9 \pm 0.1	13.0 \pm 0.1	$F_{1,239} = 37.92$, $P < 0.001$
HW (mm)	11.8 \pm 0.1	11.1 \pm 0.1	$F_{1,239} = 14.33$, $P < 0.001$
TL (mm)	73.7 \pm 0.6	64.0 \pm 0.6	$F_{1,239} = 208.9$, $P < 0.001$
AL (mm)*	24.5 \pm 1.8	25.5 \pm 2.3	$F_{1,124} = 31.12$, $P < 0.001$

SVL: snout-vent length; HL: head length; HW: head with; TL: tail length; AL: abdomen length.*The sample size was 52 (males) and 75 (females), respectively.

increased with increasing SVL did not differ between both sexes (ANCOVA, $F_{1,238} = 0.487$, $P = 0.486$; $F_{1,238} = 1.476$, $P = 0.226$, respectively), while the difference in TL was nearly significant ($F_{1,238} = 3.45$, $P = 0.064$; Figure 1).

Furthermore, females had relative larger AL than males (ANCOVA, $F_{1,124} = 31.03$, $P < 0.001$), and the rate at which AL increased with increasing SVL did not differ significantly between them (ANCOVA, $F_{1,123} = 2.07$, $P = 0.153$; Table 1, Figure 1).

3.2 Food composition A total of 93 stomachs were analyzed and 1359 prey items belonging to at least 20 families were measured (Table 2). The most common prey items were formicid, lygaeid and tenebrionid. Cannibalism was found in this species, but this was happened by chance (cannibalism rate for males and

females was 0.1% vs. 0.4%, respectively). Based on the number of identified prey, the diet composition of females and males was different ($\chi^2 = 61.28$, $df = 11$, $P < 0.001$). Females ate more formicid than males ($\chi^2 = 6.35$, $df = 1$, $P = 0.012$), while preyed lygaeid and tenebrionid similarly to males ($P = 0.095$ and 0.283). Food niche breadth for females and males was 2.89 and 3.63, respectively, and the dietary overlap was almost complete ($O = 0.989$).

Preys which volume was 0–5 mm³ and 20–30 mm³ were preferred by *P. przewalskii*, and these two categories constituting 84.3% of the total prey (Figure 2). On the basis of prey volume, the intensity that two sexes consumed the same categories was equal ($\chi^2 = 4.452$, $df = 7$, $P = 0.727$), the food niche breadth for females and males was 2.12 and 2.15, respectively, and the dietary overlap was almost complete ($O = 0.999$).

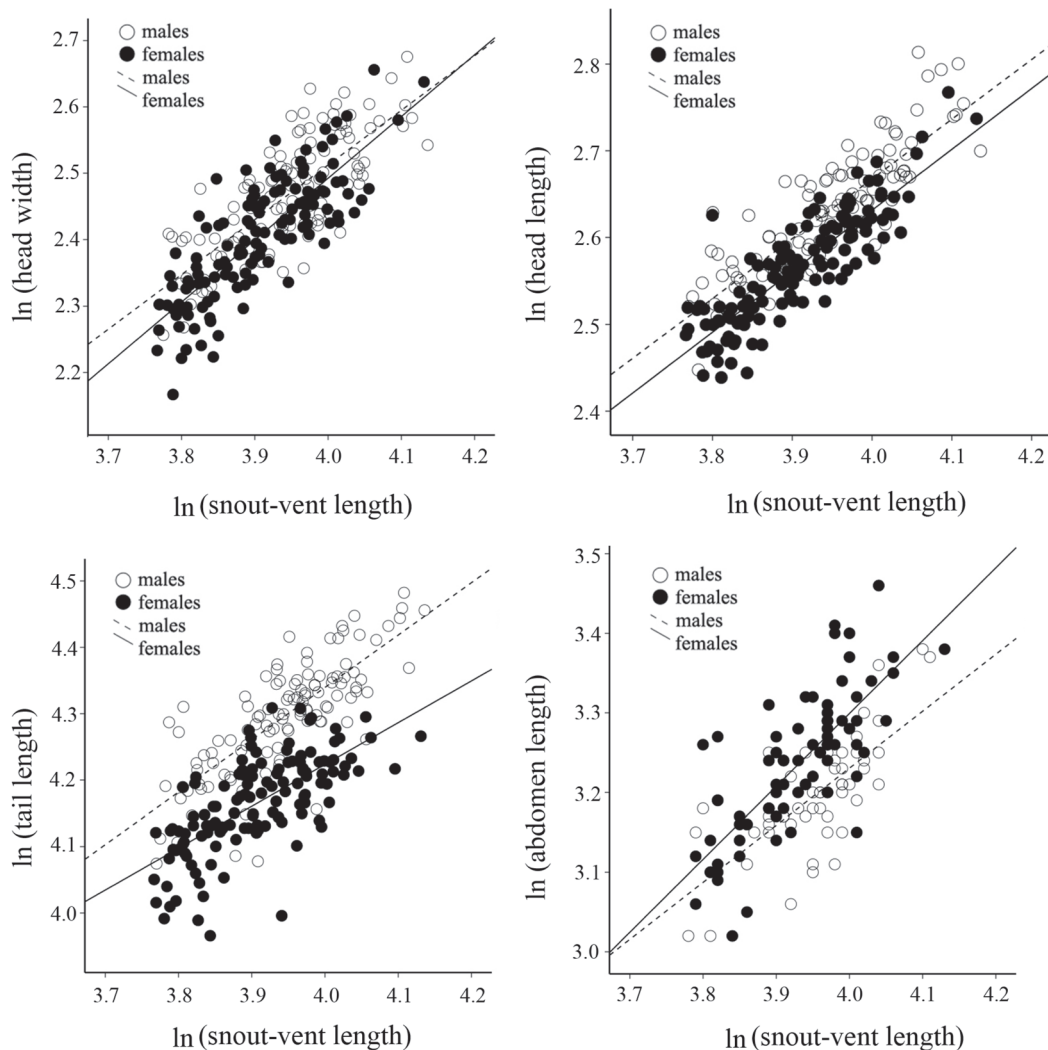


Figure 1 Linear regressions of head width (a), head length (b), tail length (c) and abdomen length (d) on SVL in *P. przewalskii*. All data were ln transformed. The sample size of abdomen for males and females is 52 and 75, respectively, while the others are 112 and 130. The black circles and lines represent females and the open circles and dash lines represent males.

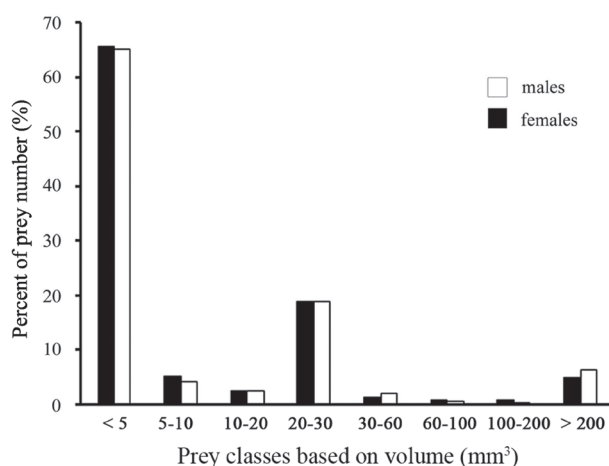


Figure 2 Distribution of prey volume classes in diets of females (873 preys) and males (486 preys) of *P. przewalskii* in the Minqin Desert, northwestern China. The figure is given based on the analysis of 93 stomachs. A total of 1359 prey items belonging to at least 20 families were measured. The prey size categories were divided according to their volume and eight classes were defined. The females were marked as black bars and the males were marked as open bars. The eight classes were: < 5 mm³, 5–10 mm³, 10–20 mm³, 20–30 mm³, 30–60 mm³, 60–100 mm³, 100–200 mm³, > 200 mm³.

3.3 Niche divergence hypothesis No significant relationship between meal size and SVL was found in males ($F_{1,38} = 1.459$, $P = 0.235$) and females ($F_{1,52} = 0.832$, $P = 0.366$), and the average meal size was similar (Table 3). The prey length and width of the largest prey item was also not correlated with SVL for males or females ($P > 0.068$ in all case), and did not differ between two sexes (ANOVA, $P = 0.814$ and 0.617 , respectively, Table 3). Furthermore, the meal size of male or female individuals did not increase with the increasing head length or head width, so did the prey length and width of the largest prey item in the stomach ($P > 0.201$ in all case). Thus, despite having relatively larger head size, males did not eat larger prey than females.

4. Discussion

4.1 Sexual dimorphism Like most other agamids (Cox *et al.*, 2007), *P. przewalskii* exhibited male biased SSD in overall body size, but unlike *P. vlangalii* which is viviparity and mainly distributed in Qinghai-Tibet Plateau (Zhang *et al.*, 2005, Jin *et al.*, 2013). In addition to the discovery of Wang and Wang (1993), male biased SSD in total limb and TL, as well as female biased SSD in AL was also found in our study.

The rate at which the examined morphological traits increased with increasing SVL did not differ significantly between male and female, indicating that SSD had been

well developed before sexual mature. Interestingly, the growth dynamics for head, tail and abdomen were different between sexes. The positive correlation between the rate of AL to HL or TL and SVL in females indicated that there was a trade-off between the growth of AL and HL or TL. Considering that males did not show that correlation, the observed trade-off might rise from the relative higher reproductive energy cost in females.

4.2 Food composition Our results showed that *P. przewalskii* was exclusive insectivorous and fed largely on insects such as formicid, lygaeid and tenebrionid. Another trophic niche study of *P. przewalskii* also pointed out the importance of formicid (Liu *et al.*, 1995). Many studies showed that formicid are a very important prey for lizard inhabited in arid environments (Al-Iohany, 1995; Pianka, 1971; Rouag *et al.*, 2007; Znari and El Mouden, 1997). This importance might due to the high occurrence and abundance of formicid in arid and desert ecosystems (Saleh and Saber, 1988), their clumped spatial distribution (Znari and El Mouden, 1997) and their high energetic value compared to other insects (Rouag *et al.*, 2007). Sporadic cannibalism was also found in both females and males, and thus judging the significance of

Table 2 Percent of prey consumed by females (n = 873 prey) and males (n = 486 prey) of *Phrynocephalus przewalskii* in the Minqin Desert, China, 2008.

Prey items			Percent		
			Females	Males	Total
Reptilia	Squamata	<i>P. przewalskii</i>	0.1	0.4	0.2
Crustacea	Isopoda	<i>Porcellio</i> spp.	0.7	1.0	0.8
Insecta	Blattoptera	unknown	0.3	1.0	0.6
	Hemiptera	Lygaeidae	31.2	24.7	28.8
		Cydnidae	0.2	0.6	0.4
		Pentatomidae	0.8	0.4	0.7
	Coleoptera	Tenebrionidae	4.8	6.2	5.3
		Carabidae	0.5	0.2	0.4
		Chrysomelidae	0.8	0.4	0.7
		Crioceridae	0.2	—	0.1
		Galerucinae	0.3	—	0.2
		Hydrophilidae	0.5	0.2	0.4
		Curculionidae	1.0	0.6	0.9
		Staphylinidae	0.5	5.8	2.4
		Coccinellidae	1.4	2.3	1.7
	Diptera	Muscidae	0.1	0.4	0.2
		Culicidae	0.1	—	0.1
		unknown	4.6	8.0	5.8
	Lepidoptera	Noctuidae	0.3	—	0.2
	Hymenoptera	Formicidae	49.4	44.7	47.7
		Vespidae	1.6	2.1	1.8
	others	unknown	0.6	1.0	0.7
	Niche breadth		2.89	3.63	3.14
	Niche overlap		0.9889		

A total of 93 stomachs were analyzed: females 54, males 39.

Table 3 Prey size and morphological traits for euthanized females (n = 54) and males (n = 39) of *Phrynocephalus przewalskii*.

	Males	Females	ANOVA/ANCOVA
Meal size (mm ³)	64.3 ± 15.8	54.0 ± 12.2	$F_{1,91} = 0.28, P = 0.599$
Prey length (mm)	11.3 ± 0.9	11.1 ± 0.6	$F_{1,91} = 0.06, P = 0.814$
Prey width (mm)	4.9 ± 0.5	5.2 ± 0.4	$F_{1,91} = 0.25, P = 0.617$
SVL (mm)	51.2 ± 0.6	49.1 ± 0.5	$F_{1,91} = 6.86, P = 0.010$
HL (mm)	13.7 ± 0.2	13.0 ± 0.1	$F_{1,90} = 10.49, P = 0.002$
HW (mm)	12.2 ± 0.2	11.4 ± 0.1	$F_{1,90} = 15.09, P < 0.001$

Meal size: the average volume of prey items encompassing in one stomach; Prey length/width: the length/width of the largest prey items in one stomach.

this phenomenon requires further study.

Although the food composition was different between two sexes, the prey size was similar. *Phrynocephalus przewalskii* mainly preyed on small insects which was less than 5 mm³, because they fed largely on formicid and lygaeid. The 20–30 mm³ preys was another preferred category, and represented by tenebrionid. Either based on prey proportion or prey size, the trophic niche overlap between two sexes was almost complete, which conformed that females and males of *P. przewalskii* did not use the resource differently.

4.3 Alternative hypothesis for SSD SSD in total size is believed to have evolved in lizards mainly because of between-sex differences in reproductive success relating to adult body size. Sexual selection is generally thought to favor larger males, either through increased success in behavioral interactions, such as male-male combat and forced mating (e.g. Shine *et al.*, 2000; Cox *et al.*, 2003). However larger female may have a fecundity advantage and fecundity selection may thus lead to female-larger SSD (Zhang *et al.*, 2005). Males of *P. przewalskii* were often observed to convolute or wag their tails during breeding season. Such display behavior always used in terrestrial defended (Qi *et al.*, 2011) and indicated that males competed to each other, at least in breeding season. SSD was also found in head size in *P. przewalskii*, with males have relative larger head. Male biased SSD in head size is thought to evolve through 3 selection pressures (Verwajen *et al.*, 2002), such as differential mating success, dietary divergence and differential growth. In our study, the hypothesis of dietary divergence could not be supported given that no differences were found in prey size between the males and females. Head size is generally related to bite force (Herrel *et al.*, 1999, 2010; Verwajen *et al.*, 2002; Vanhooydonck *et al.*, 2010). Increased head size may be related to increased bite force to win male-male contests (Gvozdík and van Damme, 2003; Husak *et al.*, 2009; Lappin and Husak, 2005), and

also may be useful in copulatory interactions (Gvozdík and van Damme, 2003). Male-male combat and male-female chase in *P. przewalskii* were frequently observed in the field during reproduction season, indicating that sexual selection might play a role in the evolution of SSD. The difference of growth dynamics for head, tail and abdomen between sexes also suggested that differential growth was present. Based on our rationation, we suggested that the SSD in head size in *P. przewalskii* might ultimately due to sexual selection and proximately to differential growth.

5. Conclusions

In summary, the present study confirmed that males of *P. przewalskii* had relative larger SVL and head size than females. However, this difference in foraging characteristics did not cause food niche divergence. Males neither forage larger nor different prey than females. Hence, the food niche divergence hypothesis was not supported by our study. Interestingly, we found that the growth rate of TL in males was larger than females, while AL was smaller. This phenomenon suggested that sexual selection and differential growth due to reproductive division may explain the observed SSD in this species.

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